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COLONIZATION OF ARTIFICIAL SUBSTRATES BY STREAM INSECTS: INFLUENCE OF SUBSTRATE SIZE AND DIVERSITY

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Abstract

A field experiment was performed in a New Mexico (U.S.A.) stream to investigate the relation between size and diversity of substrate and numbers and diversity of colonizing insects. Baskets with either small gravel, large gravel, or a 1 : 1 mixture of the two sizes were placed in a riffle area and colonization was monitored for 19 days.

Colonization was rapid, and both total number of individuals and number of species colonizing the substrates had stopped increasing by the end of the experiment. Fewer individuals colonized baskets downstream, suggesting that the drift is a major source of insect colonists. Small substrate supported more individuals and more species than the larger stones. Total number of individuals and the number of species on the mixed substrate were between numbers on small and large substrate. These results do not support previous generalizations on the relation between substrate size and complexity and the structure of invertebrate communities in streams. Results of the study are compared with the findings of recent experimental studies and it is suggested that earlier generalizations on the role of substrate size and complexity need to be reexamined.

Introduction

Substratum historically has been considered to be one of the most important factors influencing the distribution of stream invertebrates. This view developed from early observations that certain benthic species are restricted to particular types of substrate and that different types of substrate harbor assemblages of invertebrates that differ in regard to biomass, total numbers and/or numbers of taxa (Hynes, 1970).

Early workers concentrated on the relation of biomass or numbers of invertebrates to type of substrate. Much of this work was stimulated by an interest in production of stream fishes, particularly trout. In addition, the relation of type of substrate to number of benthic species received considerable attention.

Most research has concerned mineral substrates. This concern has resulted from an interest in the effects of siltation, a predictable consequence of agriculture, forestry and construction activities. The generalization that emerged from this work is that larger substrate particles support greater numbers and biomass of stream invertebrates (Tarzwell, 1936; Pennak & Van Gerpen, 1947; Ward, 1975). It has also been assumed that greater substrate size diversity is associated with a more diverse benthic fauna (Hynes, 1970). These generalizations have derived mainly from observations of the distribution of invertebrates in natural stream beds where distribution of substrate is not independent of other critical environmental factors, especially current (Nielsen, 1950).

An experimental approach to studying the role of substrate reduces the confounding effects of other variables. We report the results of a colonization experiment designed to test the effects of substrate size and diversity on numbers and diversity of stream insects. Baskets with different mixtures of substrate were placed in a stream and colonization by insects was monitored for 19 days.

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Recent work with stream faunas has profitably employed similar experimental techniques (e.g. Allan, 1975; Sheldon, 1977; Minshall & Minshall, 1977).

Methods

The study was performed in a continuous riffle area 5 m wide, 35 m long, and 0.3 m deep, located in the Rio San Antonio (35°53′N, 106°38′W, and 2330 m elevation) in the Jemez Mountains of northern New Mexico, USA. Gravel purchased in Albuquerque served as artificial substrate. Three substrate treatments were created by adding either small gravel (10 mm-25 mm), large gravel (> 75 mm), or a 1 : 1 mixture by volume of small and large to shallow 25 mm x 25 mm x 8 mm wire baskets made of 13 mm mesh galvanized screen. On 4 April 1976, 90 baskets were arranged in the riffle in 15 rows of 6 baskets each. Baskets were slightly under 1 m apart within a row and were approximately 2 m from the next row. Rows were divided into three blocks of five rows each, with every block containing ten baskets of each substrate type. Between 1200 and 1700 h on 5 April (Day 1), 6 April (Day 2), 9 April (Day 5), 13 April (Day 9), and 23 April (Day 19), two baskets of each substrate were removed from each block and the gravel was immediately emptied into plastic bags. Insects were removed from the substrate in the laboratory by washing the gravel on screens and were preserved in 70% alcohol for later identification. Number of individuals per species was determined for each basket.

The experimental design is a 3 x 5 x 3 factorial with two replicates per sub-class. Treatments are Substrate (small, large and mixed), Day, or time available for colonization (1, 2, 5, 9, and 19 days) and Block, or relative position in the riffle (upstream, middle, and downstream). Results of the experiment have been analyzed by Model I (fixed effects) 3-Way Anova. Within each block the treatments Substrate and Day were assigned at random to meet Anova's criterion of independent error terms. Converting counts of number of individual organisms and number of species to square roots stabilized variances according to the range test suggested by Bliss (1967, p. 239). Eight replicates were lost through vandalism or because stones were washed away after the current dislodged the basket. However, the design has no empty sub-classes, since every combination of treatments has at least one replicate. Because of unequal sub-class sizes in the design, Anova was performed by the method of unweighted means (Snedecor, 1956; p. 235).

Results

Twenty-four species from five insect orders are included in the analysis (Table 1). Chironomids and Simuliids, although colonizing the substrates, were not counted because of taxonomic difficulties. Gastropods and annelids have been omitted from the analysis because of very low colonization rates.

Number of Individuals

Anova reveals that all three treatments produced statistically significant effects upon the number of individual organisms colonizing the experimental substrates (Table 2). Numbers increased until Day 9 when the mean leveled off at approximately 80 organisms per basket (Fig. 1). The significant block effect results from fewer individuals colonizing baskets further downstream. Means with 95% confidence limits, based upon all baskets within each block, are: 64.3 ± 15.6 (upstream); 59.0 ± 17.6 (middle); and 39.8 ± 16.6 (downstream).

Substrate size affected the number of colonizing individuals but mixing small and large gravel did not increase the number of colonists ($F = 3.213$, $p = .079$, 3-Way-Anova of mixed vs. (small + large)); numbers of individuals on the mixed substrate treatment were between those on small and large gravel (Fig. 2). Significantly more individuals colonized small stones than large ($F = 34.302$, $p < .001$, 3-Way Anova of small vs. large.

Number of Species

Substrate and Day significantly affected the number of species, but Block had no effect (Table 3). Species richness increased most rapidly during the first day the baskets were in the stream and appears to have stopped increasing around Day 9 (Fig. 3). The decline from Day 9 to Day 19 is not statistically significant. Position of the basket within the stream had no effect upon the number of colonizing species.

Substrate size and heterogeneity influenced species richness in a manner similar to that for number of individuals (Fig. 4). Increasing substrate heterogeneity did not increase species richness ($F = 2.486$, $p = .121$, 3-Way Anova of mixed vs. (small + large)), but significantly more species colonized the smaller stones ($F = 13.004$, $p = .001$, 3-Way Anova of small vs. large).

Table 1. Stream insects identified from artificial substrates with total numbers of each taxon collected on each type of substrate

	Small Substrate	Large Substrate	Mixed Substrate
EPHEMEROPTERA			
Baetidae			
Baetis sp. 1	284	266	230
Baetis sp. 2	230	149	212
Ephemerellidae			
Ephemerella coloradensis	-	-	1
Ephemerella inermis	142	65	128
Heptageniidae			
Cinygmula sp.	32	34	28
Siphlonuridae			
Ameletus sp.	2	-	3
PLECOPTERA			
Chloroperlidae			
Alloperla sp.	93	17	27
Perlidae			
Acroneuria pacifica	36	27	37
Perlodidae			
Isoperla fulva	861	182	784
TRICHOPTERA			
Brachycentridae			
Brachycentrus sp.	21	29	13
Glossosomatidae			
Glossosoma sp.	3	1	8
Helicopsychidae			
Helicopsyche sp.	100	12	28
Hydropsychidae			
Cheumatopsyche sp.	9	16	4
Hydropsyche sp.	120	101	159
Leptoceridae			
Nectopsyche sp.	2	2	1
Philopotamidae			
Dolophilodes sp.	-	-	1
Rhyacophilidae			
Rhyacophila hyalinata	-	-	1
Rhyacophila sp.	1	6	7
COLEOPTERA			
Elmidae			
Heterlimnius corpulentus	5	7	4
DIPTERA			
Athericidae			
Atherix sp.	21	3	16
Blepharoceridae			
Philorus sp.	1	1	-
Tabanidae			
Tabanus sp.	8	-	2
Tipulidae			
Antocha sp.	-	1	-
Tipula sp.	2	-	2

Table 2. Results of 3 x 5 x 3 ANOVA of number of individuals colonizing artificial substrates.

SOURCE	SS	df	MS	F	p
SUBSTRATE	114.21	2	57.11	25.08	<.001
DAY	203.55	4	50.89	22.35	<.001
BLOCK	41.22	2	20.61	9.05	<.001
SUBSTRATE x DAY	40.00	8	5.00	2.20	.05
DAY x BLOCK	10.18	8	1.27	.56	.80
SUBSTRATE x BLOCK	.76	4	.19	.08	.99
SUBSTRATE x DAY x BLOCK	45.11	16	2.82	1.24	.29
ERROR	84.23	37	2.28		

Discussion

Our results do not support previous generalizations concerning the influence of substrate size and diversity on stream insect communities. One major departure is that fewer, not more, individuals colonized the larger substrate. This relationship is opposite from patterns observed on natural substrates (e.g. Tarzwell, 1936; Pennak & Van Gerpen, 1947; Ward, 1975). However, our results are consistent with those of Minshall & Minshall (1977) who employed similar experimental techniques and observed significantly higher total numbers on smaller substrate. Sheldon (1977) compared numbers of stream insects colonizing trays of large and small stones and found no significant effect of substrate size for any individual taxon. Minshall and Minshall also failed to show significant differences between substrate sizes when taxa were analyzed separately. These failures to demonstrate significant effects probably result from the higher variance in numbers one finds for individual taxa than for

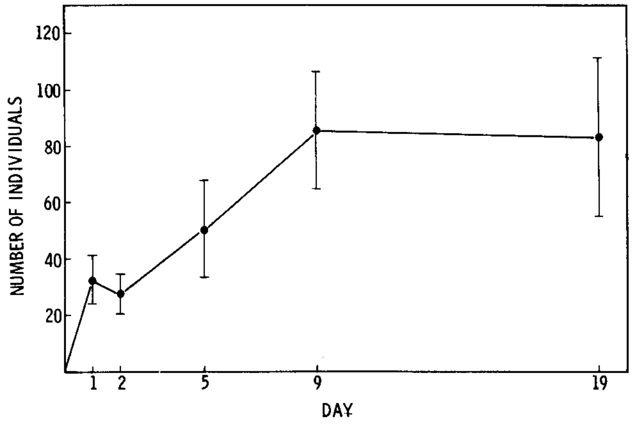

Fig. 1. Total number of individuals colonizing artificial substrates. Small, large and mixed substrate treatments are combined. Data are expressed as mean number of individuals per basket with 95% confidence limits.

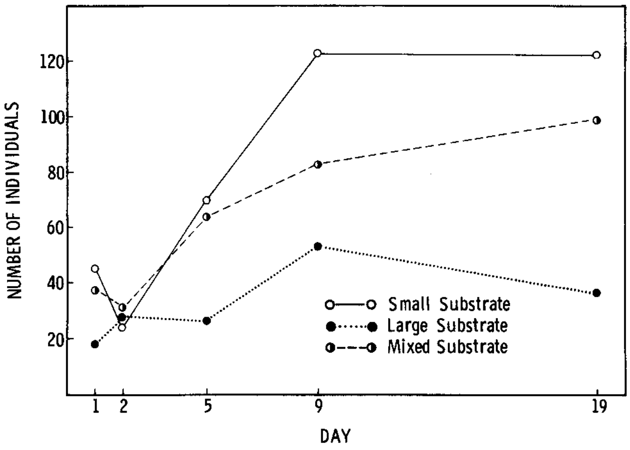

Fig. 2. Effect of substrate on number of individuals colonizing the baskets. Data are expressed as mean number of individuals per basket for each substrate treatment.

Table 3. Results of 3 x 5 x 3 ANOVA of number of species colonizing artificial substrates.

SOURCE	SS	df	MS	F	p
SUBSTRATE	2.12	2	1.06	7.19	<.01
DAY	6.10	4	1.53	10.36	<.001
BLOCK	.53	2	.27	1.80	.18
SUBSTRATE x DAY	1.25	8	.16	1.06	.41
DAY x BLOCK	.74	8	.09	.63	.75
SUBSTRATE x BLOCK	.81	4	.20	1.37	.26
SUBSTRATE x DAY x BLOCK	1.81	16	.11	.77	.71
ERROR	5.45	37	.15		

total numbers of stream insects (Hellawell, 1977). Numbers of individuals colonizing mixed substrates were between those recorded on small and large substrates (Fig. 1), which reinforces the suggestion of Minshall & Minshall that more individuals colonize smaller substrate because more surface area is available.

It was expected that mixing sizes of substrate would lead to the development of a more species-rich community. However, significantly higher numbers of species were not recorded on mixed substrates. In contrast, Allan (1975) concluded from an experimental study that more species colonized more heterogeneous mixtures of substrate. It is not clear, though, if the pattern Allan observed is statistically significant, since his experimental design did not allow the type of statistical analysis possible with the present study.

The block (position) effect observed in the present study amplifies a similar observation made by Sheldon. The decreased colonization rate observed in the lower reaches of the study riffle suggests that most colonists are drawn from the drift. If drifting organisms are the source of most colonists, then the low numbers of gastropods

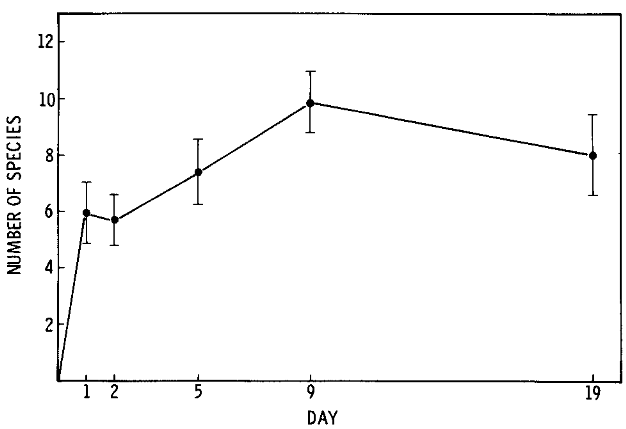

Fig. 3. Number of species colonizing artificial substrates. Small, large and mixed substrate treatments are combined. Data are expressed as mean number of species per basket with 95% confidence limits.

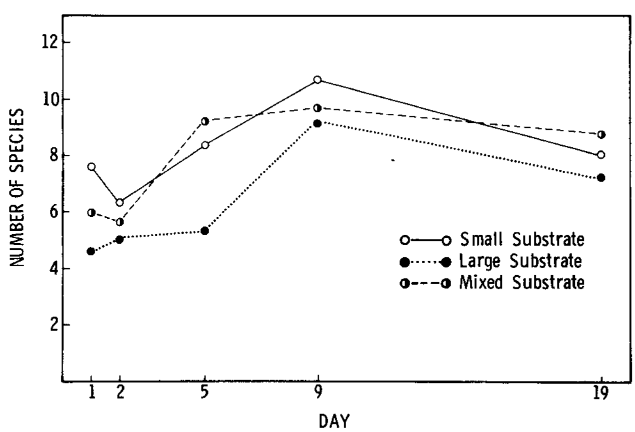

Fig. 4. Effect of substrate on number of species colonizing the baskets. Data are expressed as mean number of species per basket for each substrate treatment.

and oligochaetes on artificial substrates can be explained since these organisms are usually poorly represented in the drift.

The results of our study and those of other recent experimental studies suggest that generalizations concerning organism-substrate relations in streams need to be reexamined. We agree with the suggestion of Minshall and Minshall that future research concentrate on individual species. Studies of overall community patterns can offer useful insights; however, explanations of those patterns must be sought at the individual species level.

Discrepancies between studies of artificial and natural substrates may result from the relatively short-term nature of most colonization experiments. For example, in the present study numbers of individuals and species appeared to stabilize. However, perhaps these equilibrium numbers were temporary and successional modification of the substrate would have eventually altered numbers of individuals and species on all types of substrates. Several workers have noted that artificial substrates are modified when placed in streams (Sheldon, 1977; Minshall & Minshall, 1977; Molles, 1978). It is possible that succession would alter the three types of substrate differently and that eventually greater numbers of individuals and species would be supported in baskets with either large or mixed substrates.

On the other hand, the results of this and other recent experimental studies may accurately reflect the influence of substrate on numbers and diversity of stream invertebrates. Clearly earlier generalizations about the role of substrate size and complexity require additional testing.

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